Reproductive Investment in Four Developmental Morphs of *Streblospio* (Polychaeta: Spionidae)

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Abstract. Per brood and per offspring C and N investment were examined in four developmental morphs of the spionid polychaete *Streblospio: S. shrubsolii* (direct development, D), *S. benedicti* (lecithotrophic, L), *S. benedicti* (planktotrophic, P), and *Streblospio* n. sp. (planktotrophic, P). Large differences were apparent among these morphs in fecundity and embryo size. *S. shrubsolii* (D) and *S. benedicti* (L) invested about $10 \times$ more C and N in each offspring and 30% more C and N in each brood than did the morphs with planktotrophic development. C and N concentration (μg per unit volume) was significantly greater in *S. benedicti* (L) than in the other morphs, though no general relationship with embryo size was evident. The C:N ratio of offspring did not differ among the four morphs. Comparisons of estimated lifetime reproductive investment made by the two developmental types of *S. benedicti* indicated that lecithotrophic development involved twice the C and N investment in reproduction. Positive, significant regressions were evident between embryo C and N content and embryo volume at the inter-morph level. Significant intra-morph regressions were evident in all morphs but *Streblospio* n. sp. (P). However, the large amount of variation unaccounted for by embryo volume calls into question the use of embryo size as a predictor of parental investment in offspring.

Introduction

Three modes of development, strongly correlated with egg size and fecundity (Thorson, 1946, 1950), are recognized among marine invertebrates. Planktotrophic development is descriptive of the production of a relatively

large number of larvae, developed from small eggs, which acquire the necessary energy for growth by feeding on particulate matter during planktonic life. Lecithotrophic larvae are produced from fewer, but larger, eggs. These larvae do not feed on particulate matter but subsist, at least in part, on the energy supplied by the mother in the form of yolk during oogenesis. During direct development, offspring complete their development without a planktonic phase, usually within the mother or an egg mass; the energy for development is supplied by the mother (Thorson, 1950; Grahame and Branch, 1985).

The adaptive significance of development mode has received extensive consideration. Selection pressures such as predation, starvation, and dispersal have been proposed for development mode evolution (Thorson, 1950; Chia, 1974; Strathmann, 1985). Quantitative modeling approaches have been employed in an effort to identify the selection pressures and processes of importance in life history and development mode evolution in marine invertebrates (Vance, 1973a, b; Christiansen and Fenchel, 1979; Caswell, 1981; Grant, 1983).

One fundamental assumption of the models of Vance (1973a, b) and Christiansen and Fenchel (1979) concerns the relationship between an egg's size and its energy content. It is assumed that a positive correlation exists between an egg's measured or estimated size and the investment in material or energy that egg represents. This seemingly reasonable assumption enables the models to make use of the large amount of data on egg size and development mode available for marine invertebrates.

Interspecific comparisons of egg size and organic content including a broad range of taxa have shown the expected positive relationship to exist (Strathmann and Vedder, 1977). However, the use of interspecies comparisons to justify the assumed relationship between egg size and organic content appears invalid. McEdward and Car-

son (1987) and McEdward and Coulter (1987) have pointed out that for models describing evolutionary processes, the relevant level of variation to examine occurs within a single species. For the species of asteroids studied by McEdward, Carson and Coulter, egg size was found to be a poor predictor of organic content when examined intraspecifically due to the large amount of variation in organic content unaccounted for by egg size. Likewise, Qian (1991) found that egg size was not correlated with egg energy content within three populations of the polychaete *Capitella* sp. Variation in egg organic composition may also make egg size an unreliable predictor of an egg's energetic value (Turner and Lawrence, 1979).

To date, the relationship between egg size and egg organic content has been examined in only a small number of taxa (mostly echinoderms). One of the questions addressed in this paper concerns the extent to which the pattern identified in echinoderms is present in other taxa, specifically spionid polychaetes.

Inter- and intraspecific comparisons of reproductive and per offspring investment in organisms with different development modes have proved to be useful in identifying the ecological consequences of development mode as well as the potential evolutionary forces shaping these patterns (Menge, 1974; Perron, 1986; Levin *et al.*, 1991). The spionid polychaete genus *Streblospio*, which exhibits developmental variation both within and between species (Levin, 1984; Cazaux, 1985), offers a highly suitable system for examining questions concerning egg size and egg organic content and the consequences of development mode. Six reproductive variants are known for *Streblospio*, comprising three or more species (Levin, 1984; Cazaux, 1985; Rice, 1991; Levin and Eckelbarger, pers. comm.).

To assess the nature of reproductive costs associated with development mode patterns in *Streblospio*, both reproductive expenditure per offspring and per brood were examined in four reproductive variants. These variants are similar in body size and ecology but are distinguishable in a number of reproductive characteristics (Dean, 1965; Levin, 1984; Cazaux, 1985). Two reproductive morphs of *S. benedicti* have been identified from the Atlantic coast of the United States (Levin, 1984; Levin *et al.*, 1991). Females with planktotrophic development produce a large number (100–600) of small eggs (70–90 μm dia.) which develop into planktotrophic larvae. Lecithotrophic morphs of this species produce a smaller number (10–100) of large eggs (100–200 μm dia.) and lecithotrophic larvae (Levin, 1984). *Streblospio* n. sp. from the Gulf of Mexico also has planktotrophic development and produces a large number (100–700) of small eggs (60–70 μm dia.) (Levin, 1984; Rice and Levin, in prep.). *S. shrubsolii* with direct development from near-shore habitats in France produces a very small number (20–50) of large

eggs (200–230 μm dia.) which develop directly into crawl away juveniles (Cazaux, 1985).

Materials and Methods

Animals used during this study were obtained from three sources. *S. benedicti* with both planktotrophic and lecithotrophic development were initially collected from intertidal salt marsh habitats in Bogue Sound, North Carolina. Worms with lecithotrophic development represented second generation laboratory animals whose parents were collected in September, 1990 from natural populations at Pivers Island near Duke Marine Lab in Beaufort, North Carolina. Individuals with planktotrophic development were collected at Tar Landing Bay, North Carolina in June 1991. Individuals of *Streblospio* n. sp. were settled in the lab by S. Rice from plankton samples made in the Hillsborough River, Tampa Bay, Florida in July 1991. Individuals of *S. shrubsolii* were taken from laboratory cultures established by L. Levin in 1986 from samples collected by C. Cazaux in Arcachon, France.

Males and females of each variant were incubated in pairs at 20°C in culture dishes of sieved marsh sediment and 34–36‰ seawater, according to the techniques outlined in Levin and Creed (1986). To make observations of multiple broods from the same female it was necessary to collect recently fertilized embryos rather than eggs. Embryos are brooded on the dorsal surface in all reproductive variants and are more accessible than maturing eggs which occur within the body coelom. Embryos were always collected within 24 h of fertilization and were composed of between one (zygotes) and approximately 250 cells. The developmental stage of sampled embryos, estimated from the number of blastomeres present, was used as a covariate in data analyses.

Once embryos were separated from females they were collected by pipet, counted, and placed in a dish of filtered (0.45 μm) seawater. Two perpendicular (maximum length and width) measures of embryo diameter were made with a compound microscope and ocular micrometer for approximately 20 embryos within a brood. Embryo volume was calculated using the mean radius and the formula $\frac{4}{3}\pi r^3$ since the embryos were more spherical than prolate or oblate in form.

Entire broods, produced by a single female, were collected for C and N analysis by depositing all the embryos onto a small square of previously combusted Whatman GF/F (glass-fiber) filter paper. A minimum of approximately 15 embryos of *S. shrubsolii* (direct developer) or *S. benedicti* (lecithotrophic) and 200 embryos of *S. benedicti* (planktotrophic) or *Streblospio* n. sp. (planktotrophic) were needed to meet the detection limits of the analysis (2–3 μg of C or N). Broods smaller than these minimum sizes were not analyzed. Samples were dried

Table I

Summary of the reproductive characteristics of the four developmental morphs of Streblospio

Characters	S. shrubsolii (D)			S. benedicti (L)			S. benedicti (P)			Streblospio n. sp. (P)			df	F	P
	x̄	SD	n	x̄	SD	n	x̄	SD	n	x̄	SD	n			
Embryos/Blood	34.33ᵃ	8.15	24	50.49ᵃ	20.41	100	276.04ᵇ	93.27	26	315.20ᵇ	132.11	20	3, 103	168.93	0.0001
μg C/Brood	37.53ᵃ	12.76	24	41.15ᵃ	13.26	100	30.79ᵇ	13.83	26	26.80ᵇ	9.00	20	3, 103	8.81	0.0001
μg N/Brood	7.77ᵃ/ᵇ	1.63	19	8.50ᵃ	2.80	90	6.75ᵇ	2.22	21	5.14ᵇ	1.55	20	3, 86	8.99	0.0001
Embryo Volume															
(μl × 10⁻³)	4.67ᵃ	0.78	24	3.08ᵇ	0.44	100	0.495ᶜ	0.057	26	0.366ᵈ	0.041	20	3, 103	1395.	0.0001
μg C/Embryo	1.09ᵃ	0.25	24	0.85ᵇ	0.14	100	0.108ᶜ	0.026	26	0.091ᵈ	0.031	20	3, 103	725.4	0.0001
μg N/Embryo	0.229ᵃ	0.048	19	0.174ᵇ	0.026	90	0.023ᶜ	0.0033	21	0.017ᵈ	0.0051	20	3, 86	949.0	0.0001
C conc. (μg/μl)	233.3ᵃ	34.50	24	279.7ᵇ	51.54	100	217.2ᵃ	48.02	26	248.9ᵃ	79.7	20	3, 102	12.60	0.0001
N conc. (μg/μl)	48.67ᵃ	5.57	19	57.62ᵇ	10.19	90	45.72ᵃ	4.67	21	47.47ᵃ	12.62	20	3, 85	13.58	0.0001
C:N Ratio	4.83ᵃ	0.54	19	4.88ᵃ	0.28	90	4.97ᵃ	0.69	21	5.17ᵃ	0.48	20	3, 85	2.40	0.0767

Data on embryo volume was obtained by calculating volume $(4/3\pi r^3)$ using a mean radius determined from two perpendicular estimates of diameter. C and N data were obtained from elemental analysis of entire broods of early embryos. Degrees of freedom (df), F, and P values are listed for the ANOVA results for each character. Superscripted letters denote those values within a row which are significantly different.

in an oven at 50°C for approximately 24 h, then stored in a vacuum desiccator prior to analysis. Appropriate blank samples, without eggs, were prepared to distinguish background C and N values associated with the collection technique. The amount of C and N in each brood was determined by use of a Carlo Erba Elemental Analyzer (model E.A. 1108).

All statistical analyses of data were performed with SAS (version 5.18). All data were log transformed to remove heteroscedasticity and normalize distributions. When significant differences ($P < 0.05$) were found among the four reproductive variants, an *a-posteriori* Least Significant Difference (LSD) test was performed on means of the four reproductive types ($\alpha = 0.05$). A multiple linear regression model was used to examine the relationship between embryo volume and C and N content. Given the repeated measures structure of the data, two covariates were included in the model to distinguish between among-female and within-female variation. Covariate 1 (cov 1), representing mean values of embryo volume for each female, allowed the relationship between either C or N content and embryo volume to be examined. Covariate 2 (cov 2) was formed by subtracting the mean embryo volume of all broods produced by a female during the experiment from the mean embryo volume of each individual brood. These deviations permitted testing for a relationship between embryo C and N content and volume for multiple broods from a given female.

Results

Reproductive and offspring investment

Per brood measures of fecundity in *S. shrubsolii* (D) and *S. benedicti* (L) were significantly lower than *S. benedicti* (P) and *Streblospio* n. sp. (P), where (L), (P), and (D)

designate lecithotrophic, planktotrophic and direct development, respectively (Table 1). The differences in fecundity among reproductive morphs were accompanied by differences in embryo volume. *S. shrubsolii* (D) embryos, which were the largest of the four types (4.67×10^{-3} μl), were 12.7 × the volume of *Streblospio* n. sp. (P) embryos, 9.4 × the volume of *S. benedicti* (P) embryos, and 1.5 × the volume of embryos of *S. benedicti* (L) (Table 1). Embryo volume increased with developmental stage ($P = 0.0021$).

Comparisons of the C and N investment made to individual offspring produced by each reproductive type revealed differences similar to those found for embryo volume (Table 1). *S. shrubsolii* (D) made the largest average investment in each offspring (1.09 μg C, 0.229 μg N) followed by *S. benedicti* (L) (0.851 μg C, 0.174 μg N), *S. benedicti* (P) (0.108 μg C, 0.023 μg N), and *Streblospio* n. sp. (0.091 μg C, 0.017 μg N).

In terms of C and N, the lecithotrophic and direct developer made a greater material investment in each brood than did the morphs with planktotrophic development (Table 1). Significant differences were present in μg C per brood between *S. shrubsolii* (D) and both planktotrophic developers, and in μg C and N per brood between *S. benedicti* (L) and both planktotrophic morphs (Table I). Even though the planktotrophic morphs produced much larger numbers of embryos, the lecithotrophic and direct developers were found to have made a 30% greater C and N investment in each brood.

The C:N ratio of brooded offspring was similar among the reproductive variants, ranging from 4.83 in *S. shrubsolii* (D) to 5.17 in *Streblospio* n. sp. (P) (Table I). The C:N ratio of embryos decreased with developmental stage ($P = 0.0112$).

S. benedicti (L) exhibited significantly greater C and N concentration (μg C and μg N per μl) than the other re-

A. CARBON CONTENT VS. EMBRYO SIZE
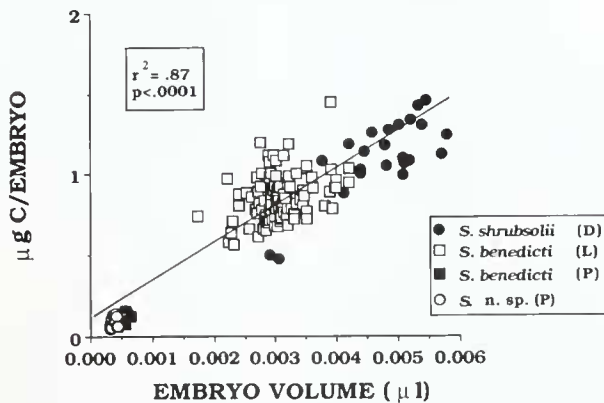
B. NITROGEN CONTENT VS. EMBRYO SIZE

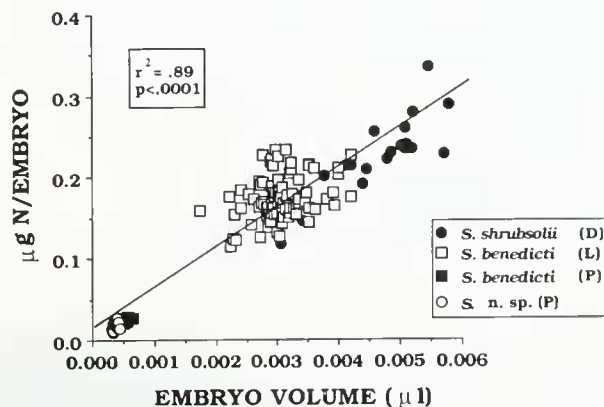**Figure 1.** Scatter plots describing the relationship between μg C/embryo (A) and μg N/embryo (B) and embryo volume for all reproductive morphs. Both regressions are highly significant ($P < 0.0001$).

productive types (Table 1). Both C ($P = 0.0306$) and N ($P = 0.0794$) concentrations decreased with developmental stage.

Embryo C and N content versus embryo volume

Significant, positive correlations were found between μg C per embryo and embryo volume ($r^2 = 0.87$, $P < 0.0001$) and μg N per embryo and embryo volume ($r^2 = 0.89$, $P < 0.0001$) across reproductive variants of *Streblospio* (Fig. 1). The regression model incorporating cov 1 and cov 2 used in analyzing the relationship between μg C (or μg N) per embryo and embryo volume explained 95% of the C variation and 97% of the N variation. A strong relationship was evident between C and N content and embryo volume across reproductive types as indicated by the significance of cov 1 in the models (C ANCOVA: $F_{1,102} = 82.34$; $P < 0.0001$; N ANCOVA: $F_{1,185} = 56.38$; $P < 0.0001$). However, the relationships between μg C and N per embryo and embryo volume within each re-

productive type were not identical. The significance of reproductive type (C ANCOVA: $F_{3,102} = 646.84$; $P < 0.0001$; N ANCOVA: $F_{3,85} = 823.51$; $P < 0.0001$) in the models indicated that differences existed among the four morphs in the nature of the regressions, specifically the y-intercept. No differences could be detected in the slope of the lines among the four types as seen by the lack of significance in the cov 1 × type interaction in both models (C ANCOVA: $F_{3,102} = 1.85$; $P = 0.1478$; N ANCOVA: $F_{3,85} = 2.29$; $P = 0.0884$). Cov 2 was significant only in the case of the N model (C ANCOVA: $F_{1,102} = 1.98$; $P = 0.1626$; N ANCOVA: $F_{1,85} = 4.37$; $P = 0.0395$), indicating that the relationship between N content and embryo volume could be detected with data from individual females sampled more than once.

Differences were evident among the four variants in the strength of the relationship between embryo C and N content and embryo volume within each morph. Significant, positive correlations existed between μg C and μg N per embryo and embryo volume for *S. shrubsolii* (D), *S. benedicti* (L), and *S. benedicti* (P), but not for *Streblospio* n. sp. (P) (Table II, Figs. 2, 3). The specific regression parameters for each of the relationships are listed in Table II. The amount of variation accounted for by the regressions, and therefore the strength of the relationship, was highest for *S. shrubsolii* (D) (71% for N content and 66% for C content). A much smaller amount of variation was accounted for by the regressions for *S. benedicti* (L)

Table II

Slope and y-intercept estimates for the regression equations of μg C and μg N/embryo versus embryo volume for Streblospio *(all morphs) and each morph separately*

Variants	y-intercept	SE	Slope	SE	P
μg C/Embryo versus Embryo Volume					
Streblospio (all morphs)	0.0431	0.0213	0.247	0.00713	0.0001
S. shrubsolii (D)	−0.102	0.187	0.256	0.0395	0.0001
S. benedicti (L)	0.489	0.0950	0.118	0.0305	0.0002
S. benedicti (P)	0.00382	0.0414	0.210	0.0831	0.0187
S. n sp. (P)	−0.00732	0.0627	0.269	0.170	0.1306
μg N/Embryo versus Embryo Volume					
Streblospio (all morphs)	0.00812	0.00431	0.0513	0.00147	0.0001
S. shrubsolii (D)	−0.0276	0.0406	0.0548	0.00855	0.0001
S. benedicti (L)	0.112	0.0187	0.0203	0.00607	0.0012
S. benedicti (P)	0.00271	0.00421	0.0402	0.00847	0.0001
S. n sp. (P)	−0.000504	0.00995	0.0489	0.027	0.0869

Estimates and standard errors (SE) are listed for the slope and y-intercept of the overall regression for *Streblospio*, including all morphs, as well as the specific regressions for each morph. P denotes the significance for each relationship.
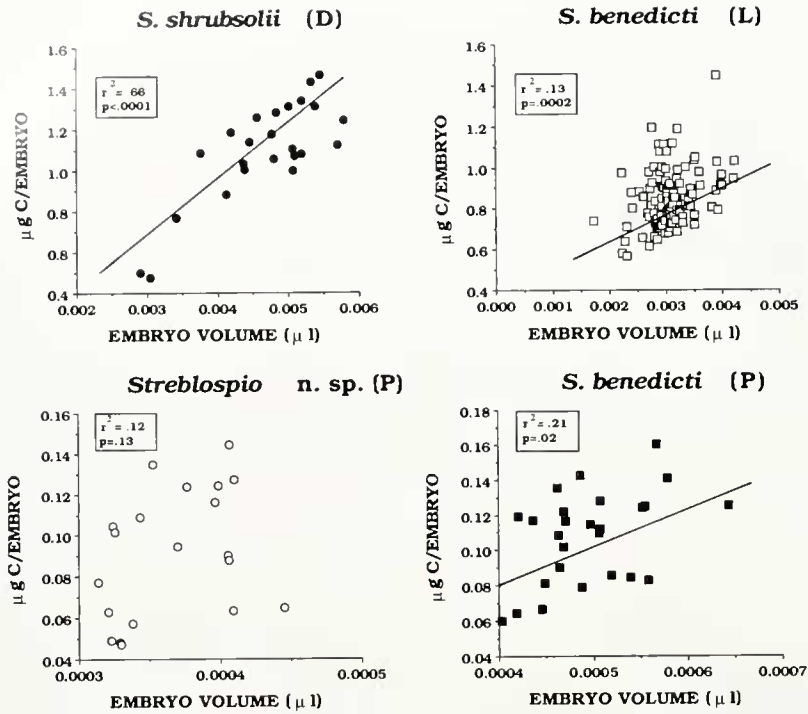
Figure 2. Scatter plots describing the relationship between μg C/embryo and embryo volume for each reproductive morph of *Streblospio*.

(11% for C and 13% for N) and *S. benedicti* (P) (21% for C and 51% for N).

A more meaningful estimate of the strength of the three significant regressions can be made by examining confidence limits for predicted embryo C and N content. Predictions of embryo C and N content using each morph's regression parameters and a single value of embryo size (each morph's mean) produced the following predicted values (±95% confidence limits): *S. shrubsolii* (D), C = 1.10 μg ± 0.31, N = 0.228 μg ± 0.058; *S. benedicti* (L), C = 0.851 ± 0.268, N = 0.174 ± 0.050; *S. benedicti* (P), C = 0.108 ± 0.050, N = 0.023 ± 0.005. These confidence intervals envelop a large portion of the range of actual values for embryo C and N content found in each of these morphs, between 53% and 99%. The large amount of variation about these regressions, which results in such large confidence intervals, makes it difficult, if not impossible, to make significantly different predictions of embryo C or N content from embryo volume within each morph.

Discussion

Offspring investment

The negative relationship between offspring size and number described for many marine invertebrate taxa (Thorson, 1946, 1950; Emlet *et al.*, 1987) including poly-

chaetes (Hermans, 1979; Levin *et al.*, 1991), was also found in this study (Table I). This tradeoff can be explained by assuming there to be a finite and limited amount of energy available for reproduction (Vance, 1973a; Smith and Fretwell, 1974; Stearns, 1976), an assumption more easily justified among closely related species which accumulate and apportion nutrients in a similar fashion. Levin *et al.* (1991) observed a negative genetic correlation between fecundity and egg size in *S. benedicti* reared in the lab, suggesting that evolutionary forces may influence this tradeoff.

The potential evolutionary forces driving differences in per offspring investment and development mode are of particular interest. One of the key preadaptations allowing for the evolution of direct from indirect development may be the evolution of a large yolk-filled egg (Wray and Raff, 1991). However, experimental embryology has demonstrated that in species developing directly, development can proceed normally at half the egg size, in a size range similar to forms with indirect development (Okazaki and Dan, 1954; Henry and Raff, 1990; Wray and Raff, 1991).

If direct development or lecithotrophy could be accomplished in *Streblospio* with only a five-fold increase over planktotrophy in per offspring investment (instead of the 10-fold increase in investment reported here), and the remaining C and N was allocated to increased fecundity, the resulting fecundity benefit could make such a
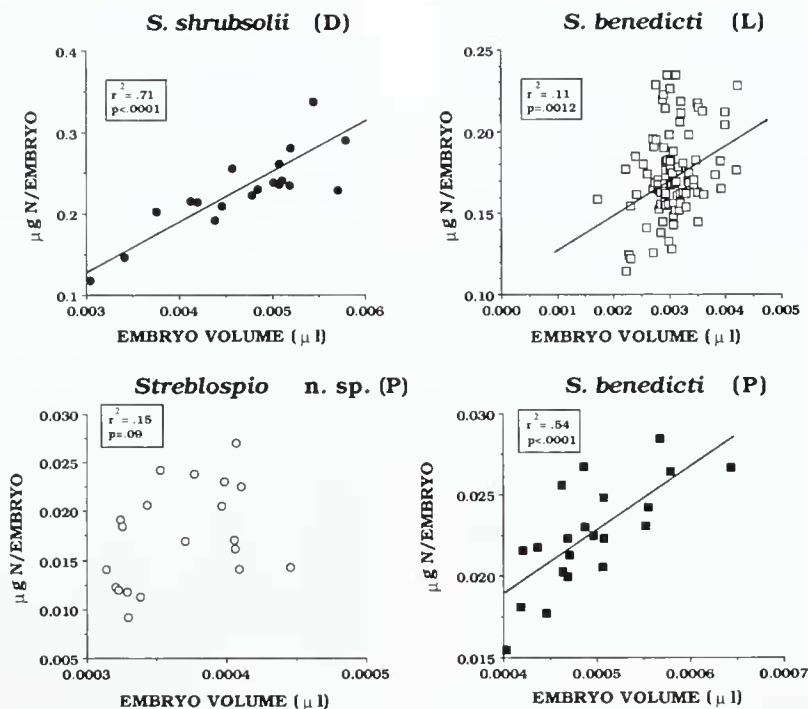
Figure 3. Scatter plots describing the relationship between μg N/embryo and embryo volume for each reproductive morph of *Streblospio.*

strategy adaptive (Table 1). However, greater per offspring investment in *S. shrubsolii* (D) and *S. benedicti* (L), in addition to developmental changes, also produces a larger offspring. *S. shrubsolii* (D) produces a 1000 μm long crawl away juvenile (Cazaux, 1985). Larvae of *S. benedicti* (L) are released and settle at half the size of *S. shrubsolii* (D) (about 550–650 μm) (Levin, 1984). Planktotrophic larvae of *S. benedicti* and *Streblospio* n. sp. are released at about 250–350 μm in length and appear to settle at a size comparable to or smaller than *S. benedicti* with lecithotrophic development (Levin, 1984).

Selection for increased offspring size may have been an important factor in development mode evolution in *Streblospio*. A shift toward larger offspring size in *Streblospio* offspring with a planktonic phase may be adaptive in the face of size-selective planktonic predation (Kerfoot, 1977; Greene, 1985; Rumrill *et al.*, 1985; Pennington *et al.*, 1986). The presumed predator avoidance behavior of some planktotrophic spionid polychaete larvae, including *S. benedicti* (P), that increase their effective size by flaring long swimming setae, is consistent with the importance of size-selective predation in this species. Larger size at settlement in *S. benedicti* (L) and at release from the female in *S. shrubsolii* (D) may also benefit offspring subject to negative interactions with permanent meiofauna or macrofauna by accelerating passage through vulnerable size ranges (Bell and Coull, 1980; Watzin, 1983, 1986). Juvenile *S. benedicti* are sensitive to interactions with

macrofauna (McCann and Levin, 1989). Levin and Huggett (1990) reported a larval and juvenile survivorship advantage in *S. benedicti* (L) (relative to *S. benedicti* (P)) during a field study of populations of *S. benedicti* with lecithotrophic and planktotrophic development.

Offspring composition

Even though morphological distinctions are evident in yolk granules of *S. benedicti* with lecithotrophic and planktotrophic development, differences in gross measures of organic composition were not evident in this study (Eckelbarger, 1980, 1986). Offspring C:N ratios of the four reproductive types could not be distinguished statistically, suggesting that the relative proportion of protein to non-nitrogen containing compounds is the same among the four morphs (Table 1). Turner and Lawrence (1979) also found that organic composition did not change with egg size in the echinoderms they studied. Lawrence *et al.* (1984) concluded, due to the compositional similarity of eggs of different sizes and development modes, that the significance of larger eggs was not to accommodate differences in the energetic demands of development, but to create a larger offspring. One would expect to see a higher proportion of lipid in larger eggs if the change in development involved a greater energetic demand (Lawrence *et al.*, 1984). Increased per offspring investment in *Streblospio* may have similar importance, *i.e.*, the production of larger offspring.

C and N concentration (μg/μl) was similar among the embryos of three of the four *Streblospio* reproductive morphs, and no consistent trend with embryo size was noted (Table I). Qian and Chia (1992) found that egg energy concentration was similar in lecithotrophic and planktotrophic *Capitella* sp. Strathmann and Vedder (1977) reported that organic matter per unit volume decreased with egg size in echinoderms with feeding larvae. Such a trend has not been observed in echinoderms with larger eggs, including pelagic lecithotrophs (Turner and Lawrence, 1979; McEdward and Chia, 1991). Energy concentration does appear to be significantly greater in eggs of echinoderms with nonfeeding larvae than those with feeding larvae (Emlet *et al.*, 1987; McEdward, pers. comm.); this observation is consistent with data presented by Needham (1963). Thus, important fundamental differences may exist among the eggs of echinoderms with different developmental modes. More data are required before such trends can be discerned for polychaetes.

Reproductive investment

The lecithotrophic and direct developers made greater material investments in each brood than either planktotrophic developer. In addition to investing more C and N in each offspring, *S. benedicti* (L) was also found to have invested 33% more C and 26% more N in each brood than did *S. benedicti* (P). However, these values are minimum estimates of the difference in reproductive investment since *S. benedicti* (P) produced more broods that were too small to be analyzed for their C and N content. Lifetime investment levels can be estimated by combining data on per offspring investment made in this study with lifetime fecundity data made by Levin *et al.* (1987), where worms were raised under the same experimental conditions. Using these data, *S. benedicti* (P) (1324.32 eggs/lifetime) would have a calculated lifetime reproductive investment level of 143.03 μg C and 30.46 μg N, and *S. benedicti* (L) (336.6 eggs/lifetime) would have invested 286.45 μg C and 58.57 μg N. Based on these calculated values, *S. benedicti* (L) makes a two-fold higher investment in reproduction than *S. benedicti* (P). These estimates do not technically represent reproductive effort since reproductive effort is defined as the proportion of resources devoted to reproduction (Havenhand and Todd, 1989). However, the similarity of these two morphs in size as well as ecology (Levin *et al.*, 1987; Levin and Huggett, 1990), would suggest that such estimates may represent a first approximation of reproductive effort, though some caution is warranted (Grahame, 1982). Efforts at determining which reproductive pattern, planktotrophy or lecithotrophy, is more energetically expensive have yielded equivocal results (Grahame and Branch, 1985; Strathmann, 1985).

Differences in apportionment of energy to growth and development in *S. benedicti* with planktotrophic and lecithotrophic development may partially account for the difference in reproductive investment. *S. benedicti* with planktotrophic development reaches sexual maturity (first reproduction) earlier and at a larger size than the lecithotrophic morph, indicating that growth and developmental rates are accelerated in planktotrophs compared to lecithotrophs (Levin *et al.*, 1987; Levin *et al.*, 1991). The importance of accelerated growth and development in planktotrophic *S. benedicti* is further suggested by demographic analyses of the two developmental morphs. Similarity in estimated population growth rates (λ) in the two morphs were the result of a balance between a larval and juvenile survivorship advantage in lecithotrophs and increased fecundity in early adult stages in planktotrophs (Levin *et al.*, 1987; Levin and Huggett, 1990). Given the effect of age at first reproduction and early fecundity on population growth rates (Stearns, 1976), females with planktotrophic development may be investing in future offspring both through energy committed to eggs directly and through enhanced early growth and development. The evolutionary shift from planktotrophy to lecithotrophy may involve not only changes in offspring size and investment, but also age and size at maturity in *S. benedicti*.

Embryo size versus C and N content

Significant, positive relationships have been found between egg size and organic content using data from a number of species in this study (Fig. 1) as well as others (Strathmann and Vedder, 1977; Turner and Lawrence, 1979; McEdward and Chia, 1991). In general, the strength of this relationship when examined at the interspecific level, as reflected by r^2 values, appears to be high (present study; McEdward and Chia, 1991). However, large errors in prediction may result when using regression equations formulated with interspecific data to predict values of per offspring investment from intraspecific and intra-morph data on embryo size (Bridges, 1992). The strength of intra-morph relationships between embryo C and N content and embryo volume ranged from *S. shrubsolii* (D), where the regressions accounted for 66% of the variation in C and 71% of the variation in N to *Streblospio* n. sp. (P), where significant relationships could not be detected (Figs. 2, 3). Even in the three morphs where significant regressions were evident, the size of 95% confidence intervals on predicted values of C and N content would preclude making significantly different predictions of C and N content from embryos of different size within developmental morphs. Observations in this study of lecithotrophic and planktotrophic polychaetes are similar to those in echinoderms with lecithotrophic development where variation

among species in the nature and strength of the relationship between egg size and organic content has been found (McEdward and Carson, 1987; McEdward and Coulter, 1987; McEdward and Chia, 1991). Given that egg or embryo size accounts for minimal variation in organic content within species, considerable caution should be taken in presuming egg or embryo size as an accurate measure of per offspring investment.

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